

STUDIES ON
THE AUDOUINELLA MICROSCOPICA (NAEG.)
WOELK. COMPLEX (RHODOPHYTA)

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Several recent studies (Abbott 1962, West 1968, Woelkerling 1970, 1971) have indicated that the taxonomic status of numerous species in the *Audouinella* complex (*Acrochaetium-Rhodochorton* complex) of the red algae is in need of review. Many of these taxa have been described from meagre material and (or) without regard for possible intraspecific variation, and recent work on several species (Abbott 1968, West 1969, Woelkerling 1970) has resulted in a reduction of some taxa to synonymy.

Preliminary work of the author on the audouinelloid algae of the New England coast of North America has led to a detailed consideration of the relationships of *Audouinella microscopica* (Naegeli) Woelkerling to six closely related taxa: *Acrochaetium crassipes* Boergesen (1909, p. 1, Fig. 1; 1915, p. 20, Figs. 11-13), *A. catenulatum* Howe (1914, p. 84, pl. 31, Figs. 12-18), *A. microfilum* Jao (1936, p. 240, pl. 10, Figs. 1-5), *Kylinia collopoda* (Rosenvinge) Kylin (see Rosenvinge 1898, p. 41, Figs. 10-11; 1909, p. 81), *K. compacta* (Jao) Papenfuss (see Jao 1936, p. 241, pl. 10, Figs. 6-14), and *K. moniliformis* (Rosenvinge) Kylin (see Rosenvinge 1909, p. 98, Figs. 28-29). (It should be noted here that although the taxonomic proposals of Woelkerling (1971) have been adopted in this study, older generic names have been employed in cases of probable synonymy in order to avoid making new and unnecessary nomenclatural combinations). *A. crassipes* and *A. catenulatum* were described respectively from material collected in the Virgin Islands (Boergesen 1909) and Peru (Howe 1914) while the other four taxa have been described from or are reported to occur along the New England and adjacent coasts.

These seven species have been distinguished from one another on slight differences in habit, branching, cell size,

chromoplast shape, and spore size. These apparent differences, however, may not be as taxonomically reliable as formerly thought, and Woelkerling (1971) has suggested that several or all of the taxa under discussion may be conspecific. The aims of the present investigation have been: 1) to critically examine and compare morphologically the type collections and other populations of these seven taxa, and 2) to clarify taxonomic limits within this species complex, particularly with reference to the New England flora.

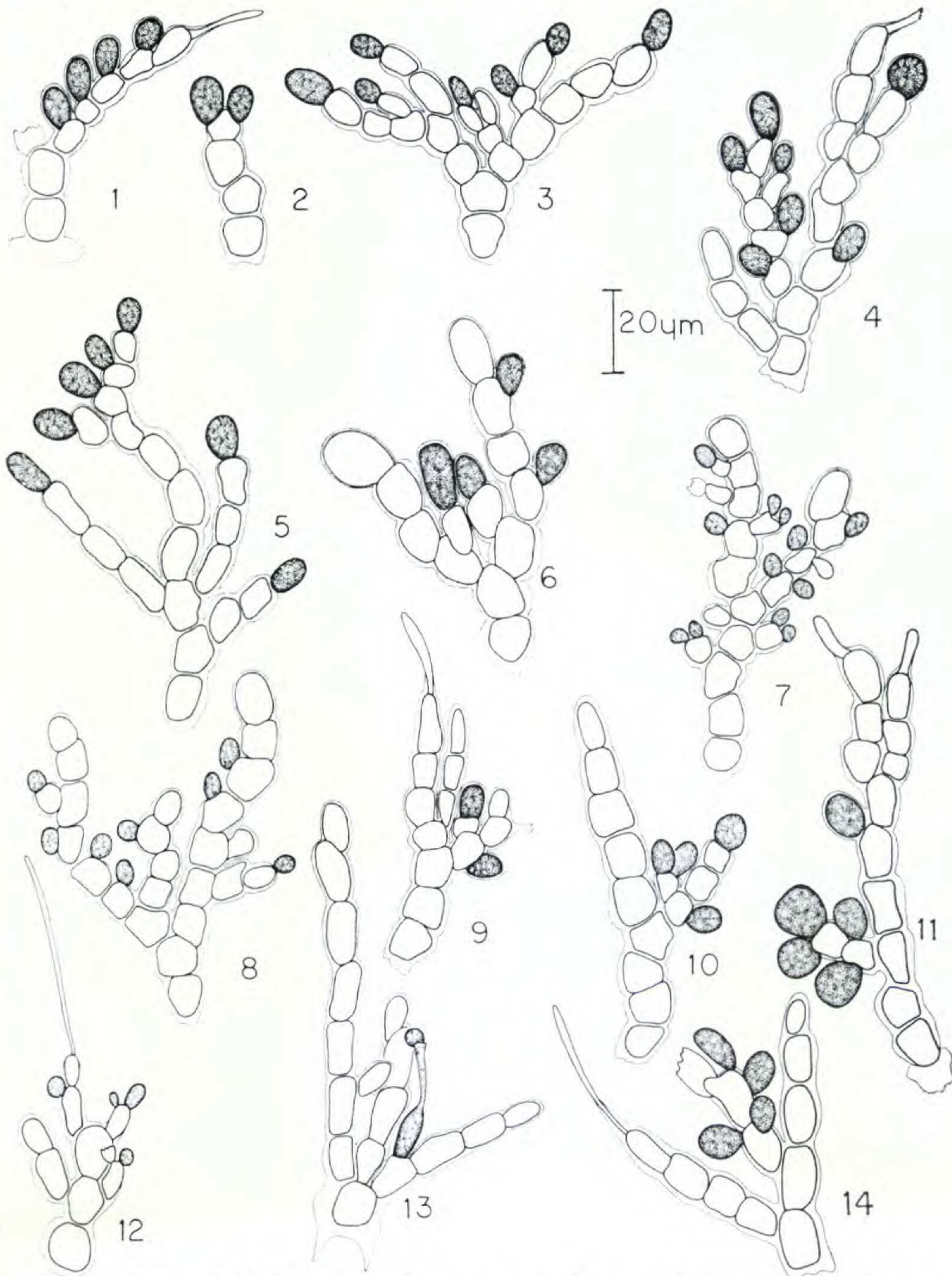
MATERIALS AND METHODS

The morphological techniques employed in these studies have been detailed elsewhere (Woelkerling 1970). Line drawings have been made with the aid of a Leitz drawing head microscope attachment; herbarium abbreviations follow Lanjouw and Stafleu (1964).

Wherever possible, results have been based on the study of populations (Table 1) rather than isolated individuals. This approach has been facilitated by the nature of the material; i.e., audouinelloid algae sometimes occur in large numbers on various substrates and by virtue of their small size, dozens or hundreds of individuals may be present in a single collection. The data presented here in most cases represents the results of study on numerous individuals within each population; an exception is the type collection of *Acrochaetium crassipes* Boergesen which is represented in C only by several drawings. Data on this taxon has been taken from the accounts of Boergesen (1909, 1915).

MORPHOLOGY

Audouinella microscopica, the earliest described member of this complex, was first characterized by Kuetzing (1849), and later Naegeli (1861) discussed and illustrated it in somewhat greater detail. Although Kuetzing (1849, p. 640) cited the Bay of Naples as the type locality, Hamel (1927; 1928) has indicated that the type collection came from Torquay, England and is represented by specimen 454 in Hauck and Richter's "Phykothea Universalis" (as *Chan-*



Figs. 1-14. *Audouinella microscopica* (Naegeli) Woelkerling. Figs. 1-6. Monosporangial plants from type collection. Note variation in habit and in development of basal cell wall. Figs. 7-8. Spermatangial plants from type collection. Figs. 9-11. Cystocarpic plants from type collection. Note remains of trichogyne and an apparent transversely divided carpogonium (Fig. 9). Figs. 12-14. Sexual plants from Denmark removed from the host, *Chordaria*. Note variation in development of basal cell wall and carpogonium with attached spermatium (Fig. 13).

transia secundata (Lyngbye) Thuret). The type specimen in the Kuetzing collections at L contains only plants collected by Naegeli in England (identical to those distributed in Hauck and Richter) and none from the Bay of Naples. The location given by Kuetzing (1849) is, therefore, apparently in error.

Plants from the type collection of *A. microscopica* in L as well as isotypes in FH and NY have been examined during this study. The plants form a dense population on *Enteromorpha* (Chlorophyta), are 40-100 (-200) μ tall, and are attached to the host by unicellular bases with or without enlarged lower cell walls (Figs. 1-11). One or occasionally several erect filaments arise from the basal cell (Figs. 3, 4), and these may remain unbranched (Fig. 1-2) or bear several secundly or irregularly arranged laterals (Figs. 3-11). Cells are doliiform to cylindrical in shape, 6-8 (-12) μ wide and 6-12 μ (1-2 diameters) long; terminal hairs up to 40 μ long occur occasionally.

Both monosporangial and sexual plants are present in the material examined. The monosporangia occur singly or in pairs, are 7-10 μ long and 5-7 μ wide, are sessile or stalked, and are scattered over the erect filaments (Figs. 1-6). Spermatangia are ovoid, up to 4 μ long, occur singly or in pairs, are sessile or stalked and are scattered over the erect filaments (Figs. 7-8). Unfertilized carpogonia have not been observed definitely in the type collection material, but the remains of at least one apparently transversely divided fertilized carpogonium has been seen (Fig. 9). Gonimoblasts are several celled and give rise to terminal or lateral carposporangia 7-10 μ long and 6-8 μ wide (Figs. 10-11). Only the clustered arrangement of the carposporangia distinguishes the gonimoblast from a monosporangial bearing branch. Tetrasporangial individuals have not been observed but are reported by Schiffner (1931).

Hamel (1927, 1928) previously reported sexual individuals, and Lund (1942) noted possible antheridia in Danish plants. One Danish collection on loan from Dr. Lund has been examined and found to contain numerous sexual in-

dividuals including specimens with carpogonia bearing attached spermatia (Figs. 12-14). Lund (1942) referred the Danish material to *Chantransia* (= *Kylinia*) *collopoda*, a taxon here considered conspecific with *Audouinella microscopica*.

Monosporangial plants more or less agreeing with the above description of *A. microscopica* occur along the New England and adjacent coasts, but up to the present time, they have been referred (Edelstein & McLachlan 1966; Edelstein et. al. 1967; Jao 1936; Taylor 1937, 1957) to four other species (see above) including two (*A. microfilum* and *K. compacta*) with type localities in the Cape Cod region. An analysis (Table 1) of a number of New England populations including those cited by the above authors, strongly indicates that they agree in all essential features with *A. microscopica* and are therefore justifiably referred to that species.

The analysis further indicates that while the range in basal attachment, height, branching, number of erect axes, chromoplast shape, cell size, and spore size may vary somewhat from one population to the next (probably attributable to variation in environmental factors and age), considerable overlap in these characters exists between various collections and in no cases can distinct specific limits be drawn. Consequently, it appears that all these plants are best regarded as members of a single, variable species — *A. microscopica*. Woelkerling (1971) has found similar variation in southern Australian populations of this species.

Ecological data on *A. microscopica* in New England remains scant. Specimens have been collected from July through February, but the species probably occurs throughout the year and has thus far escaped detection by virtue of its small size. Sexual plants have not been reported to date in New England, and indeed have been recorded only twice from European waters. *A. microscopica* has been found growing on a number of algae in New England waters (*Chaetomorpha*, *Chondria*, *Chondrus*, *Chordaria*, *Cladophora*, *Entromorpha*, *Polysiphonia*, *Porphyra*) all of which

occur in the sublittoral or in the drift. The species no doubt enjoys a much wider host distribution and is to be sought particularly on old and heavily epiphytized algae.

SYSTEMATIC IMPLICATIONS

The results of this study again (see Woelkerling 1971) raise the question as to whether a number of taxa closely related to *Audouinella microscopica* are really distinct species. The type collections of six of these taxa have been available for study, and a detailed analysis (Table 1) strongly indicates that taxonomic distinctions cannot be made among them on the bases of height, number of erect axes, cell size, or spore size. As is the case for the various New England collections, considerable overlap in the above characters is evident in the type collection populations, and specific limits cannot be clearly drawn. Moreover, a comparison of the type collection illustrations (see Boergesen 1909; Howe 1914; Jao 1936; and Rosenvinge 1909) also indicates the great similarity of these taxa.

In addition to the above characteristics, apparent differences in habit, development of the basal cell wall, degree of branching, origin of laterals, chromoplast shape, presence or absence of hairs, and position of sporangia have been used in making specific distinctions. As Woelkerling (1971) has shown in a lengthy review, the degree of branching, presence or absence of hairs, and sporangial position are not taxonomically reliable in general for making specific distinctions in the *Audouinella* complex, and the present study supports this view. Thus, for example, the type collection of *A. microscopica* contains plants which vary in the degree of branching, may or may not have unicellular hairs, and possess both terminal and lateral sporangia (Figs. 1-11).

Hamel (1927, 1928) attempted to distinguish *A. microscopica* from other members of this complex on the basis of lateral branch origin. Thus, according to Hamel, the first lateral branch in *A. microscopica* always arises from the first cell above the base. The type collection of this species,

however, also contains unbranched plants (Figs. 1-2) and plants in which the lateral arises from the basal cell (Fig 4) or from two or more cells above the base (Figs. 9-11). Woelkerling (1971) found similar variation in Australian populations of *A. microscopica*, and this variation also occurs in New England populations. Thus it appears that specific distinction based on origin of lateral branches is not taxonomically reliable.

The presence of a much enlarged basal cell wall has been used (Rosenvinge 1898, 1909; Lund 1942) to distinguish *Kylinia collopoda* from *Audouinella microscopica*. However, considerable variation in basal cell wall development occurs in the type collection of *A. microscopica* (Figs. 1-11) as well as collections made by Lund (Figs. 12-14), and Woelkerling (1971) reported a similar situation in southern Australian populations of this species. This variation suggests that this character also is not taxonomically reliable for delimiting species in this complex.

Chromoplast shape (parietal vs. stellate) has also been used (Taylor 1957) to distinguish these species. However, recent work (West 1968, p. 92, 95; Woelkerling 1971) has indicated that plastid shape shows considerable intraspecific variation and therefore is not a generally trustworthy taxonomic criterion. Some variation has already been recorded in plastids of *A. microscopica* (Woelkerling 1971), and studies (e.g., Abbott 1962, p. 100; Boergesen 1937, p. 39, 41; Drew 1928, p. 156, 176, 177, 182; Feldmann 1962, p. 220; Levring 1937, p. 94) have noted similar variation in other species. It appears, therefore, that the taxa under discussion cannot be distinguished from one another solely on apparent differences in chromoplast shape.

This study has not revealed any other criteria by which these taxa may be reliably separated into distinct species; consequently all are regarded here as conspecific with *Audouinella microscopica*.

The relationships of *A. microscopica* to four other taxa remain uncertain, primarily because the type collections have not been available for examination. The taxa include

Chantransia mediterranea Levring (1942, p. 30, Figs. 1a-g), *C. minutissima* Reinsch (1874-5, p. 33, tab. V, Fig. 2a, tab. XI, Fig. 3a; not of other authors), *C. trifila* Buffham (1892, p. 24, pl. 3, Figs. 1-4), and *Kylinia scapae* Lyle (1929, p. 245, Figs. 6-7). A comparative examination of the type collections of these taxa will almost certainly show them to be conspecific with *A. microscopica*. The androphores described and illustrated by Lyle (1929) probably represent young, unelongated unicellular hairs.

COLLECTIONS EXAMINED

Types and Isotypes: DENMARK: Kattegat Channel, 17. vii. 1890, *Rosenvinge* (C, Rosenvinge 863, Algae marinae Danicae, type of *Chantransia moniliformis* Rosenvinge). ENGLAND: Torquay, 1845, *Naegeli* (L 940285 . . . 306, type of *Audouinella microscopica* (Naegeli) Woelkerling). Torquay, 1845, *Naegeli* (FH, No. 454, "Phykotheke Universalis", isotype of *A. microscopica*). Torquay 1845, *Naegeli* (NY, No. 454, "Phykotheke Universalis", isotype of *A. microscopica*). GREENLAND: Holstenborg, 9. vii. 1895, *Hanson* (C, type of *Chantransia collopoda* (Rosenvinge) Rosenvinge). PERU: La Punta, region of Callao, 25. i. 1907, *Coker* (NY, type of *Acrochaetium catenulatum* Howe). UNITED STATES: Black Rock, Sconticut Neck, New Bedford, Massachusetts, 25. vii. 1934, *Jao* (MICH, Woods Hole, No. 275, type of *Acrochaetium compactum* Jao). Norton Point, Martha's Vineyard, Massachusetts, 3. viii. 1934, *Jao* (MICH, Woods Hole, No. 280 [not 274 as reported by Jao 1936, p. 240], type of *Acrochaetium microfilum* Jao). VIRGIN ISLANDS: St. Thomas (The Harbour), i. 1906, *Boergesen* (C, type of *Acrochaetium crassipes* (Boergesen) Boergesen).

Other collections: DENMARK: Vorupor, NW coast of Jutland, 30. vii. 1929, *Lund* (C). MASSACHUSETTS: Cape Codder Point (Falmouth), 19. xi. 1969, *Woelkerling* (2292, personal collection). West Falmouth Harbor, 17. x. 1970, *Woelkerling* (2826, personal collection). Woods Hole (Nobska Point), 4. ii. 1970, *Woelkerling* (2320, personal

collection). NOVA SCOTIA: Cranberry Cove, 12. ix. 1965, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 1867, as *Acrochaetium microfilum* Jao). Herring Cove, 18. i. 1966, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2217, as *Kylinia compacta* (Jao) Papenfuss). Ketch Harbour, 7. ii. 1966, *McLachlan & Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2244, as *Kylinia collopoda* (Rosenvinge) Papenfuss). Peggy's Cove, 26. viii. 1965, *Edelstein* (Nat. Res. Council. Herb., Halifax, No. 2105, as *K. collopoda*).

SUMMARY

The relationship of *Audouinella microscopica* to six closely related taxa has been investigated with particular reference to the New England and adjacent coasts. The morphology of monosporangial and sexual plants in the type collection of *A. microscopica* is discussed and illustrated. Collections from the New England region previously referred to *Acrochaetium microfilum* Jao, *Kylinia collopoda* (Rosenvinge) Kylin, *K. compacta* (Jao) Papenfuss, and *K. moniliformis* (Rosenvinge) Kylin have been found to represent specimens of *Audouinella microscopica*. A comparative study of the type collections of these five taxa as well as *Acrochaetium crassipes* Boergesen and *A. catenulatum* Howe indicates that all taxa are conspecific with *Audouinella microscopica*. *Chantransia mediterranea* Levring, *C. minutissima* Reinsch non. al., *C. trifila* Buffham, and *Kylinia scapae* Lyle are regarded as probable synonyms.

ACKNOWLEDGMENTS

Sincere thanks are due Dr. T. Edelstein (Atlantic Regional Laboratory, National Research Council, Halifax, Nova Scotia), Dr. I. Mackenzie Lamb (FH), Dr. Soren Lund (C), Dr. W. F. Prud'homme van Reine (L), Dr. Clark Rogerson (NY), and Dr. W. R. Taylor (MICH) for the loan of herbarium material. Miss Susan Heller kindly aided in the preparation of the drawings. This work was supported in part by National Science Foundation Grant GB-13250 to the Systematics-Ecology Program.

Contribution No. 242 from the Systematics-Ecology Program, Marine Biological Laboratory.

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TABLE I. MORPHOLOGICAL DATA ON POPULATIONS
OF *A. MICROSCOPICA COMPLEX*¹

No.	Name	No. of Erect Axes	Height	Cell Width	Cell Length	L/W Ratio	Spore Length	Spore Width
1	"CATENULATUM"	1	40-140 μ	7-11 μ	7-10 μ	1	9-11 μ	6-7 μ
2	"COLLOPODUM"	3	20-200 μ	7-9 μ	10-15 μ	2-4	8-15 μ	7-8 μ
3	"COMPACTUM"	(2-)3(-4)	20-50 μ	5-8 μ	5-10 μ	1-2	6-8 μ	5-7 μ
4	"CRASSIPES"	1 (-2)	40-60 μ	5-7 μ	5-9 μ	1-2	6-8 μ	5-7 μ
5	"MICROFILUM"	3-4	20-40 μ	3-6 μ	4-7 μ	1	6-8 μ	4-6 μ
6	"MICROSCOPICUM"	1 (-2)	40-200 μ	6-12 μ	6-12 μ	1-2	7-10 μ	5-7 μ
7	"MONILIFORMIS"	2-3	40-150 μ	7-11 μ	7-14 μ	1-2	11-15 μ	6-7 μ
8	N. England Populations	1-4	20-100 μ	3-10 μ	3-11 μ	1-2	6-15 μ	4-9 μ
9	Australian Populations	1-3(-4)	20-140 μ	3-12 μ	3-10 μ	.75-2	5-10 μ	4-7 μ

¹Data for the first seven populations is based on an examination of the type collections of those taxa; No. 8 represents a composite of data from all New England collections examined; No. 9 represents data from Woelkerling (1971).